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Host–parasite community interactions in a human-modified habitat (人為的攪乱を受けた生息環境における宿主–寄生虫間の交渉)

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Parasites contribute greatly to biodiversity but we still lack coverage of parasites in wildlife across both their geographic and host ranges. My thesis uses Bornean primates and their gastrointestinal helminth parasites as a model system to: 1) describe host-parasite community associations in a key study system that lacks such information; 2) determine patterns of host specificity and generalism by exploring the extent to which parasites are shared across hosts; and, 3) identify factors that influence the diversity and distribution of parasites in a human-modified landscape – the Kinabatangan floodplain – in Sabah, Malaysia.

In **chapter 2**, I characterize the parasite assemblages of a community of Bornean primates, including representatives of most primate families that currently exist in the Old World outside of Madagascar (Lorisidae, Tarsiidae, Cercopithecidae, Hylobatidae, Hominidae), with many species being endemic to the island and most threatened to some extent. Through parasitological analyses, and by using several measures of parasite infection as proxies for parasite diversity and distribution, I show that 1) most parasite taxonomic groups infect most primate species, 2) parasite infracommunities of nocturnal primates differ from the others, reflecting both phylogenetic and ecological constraints, and 3) soil-transmitted helminths (STH) are more abundant within the host community than trophically-transmitted parasites. In terms of expanding the current knowledge of primate parasites, this work provides new records for southern pig-tailed macaques, silvered langurs and Western tarsiers in the wild, while adding to the limited records for the other primate species in the community.

In **chapter 3**, I focus on a specific parasite, *Lemuricola (Protenterobius) nycticebi*, the only pinworm species known to infect strepsirrhine primates outside Africa, and the only pinworm species yet described in slow lorises. This study provides a detailed morphological comparison of female and male worms, and a first description of fourth-stage larvae collected from free-living slow lorises (*Nycticebus menagensis*) in Sabah, Malaysian Borneo. Using mitochondrial and nuclear markers, I also reconstructed the species' phylogenetic relationship with other pinworms infecting primates. Both morphological and molecular results indicate a distinct association between *L. (P.) nycticebi* and its host. However, while taxonomy identifies this species as a member of the *Lemuricola* clade and grouped pinworms infecting lemurs and slow lorises together, phylogenetic reconstruction splits them, placing *L. (P.) nycticebi* within the *Enterobius* clade. These results suggest that *L. (P.) nycticebi* may represent a different taxon altogether, and that it is more closely related to pinworm species infecting Old World primates outside Madagascar. *Pongobius pongoi* (Foitová *et al.* 2008) n. comb. is also proposed.

Chapters 4 and 5 look at two genera of STH nematodes reported from several primate species in Africa and Asia: *Strongyloides* and *Oesophagostomum*. In the first study, I describe a case of infection with a cryptic species of *Strongyloides* in a Bornean slow loris living within a diverse community of several primate

species. Fresh fecal samples were collected from five primate species and nematode larvae cultured from these samples were selected for phylogenetic analyses. Sequences obtained for most larvae were identified as *S. fuelleborni*, grouping into three different clusters and showing no aggregation within specific hosts or geographic location. In contrast, a set of parasite sequences obtained from a slow loris clustered closely with *S. stercoralis* into a different group, being genetically distinct to sequences reported from other primate hosts, humans included. These results suggest that although *S. fuelleborni* infects all haplorrhines sampled in this primate community, a different species might be infecting the slow loris, the only strepsirrhine in Borneo and one of the least studied primates in the region. Although more data are needed to support this conclusion, I propose that *Strongyloides* species in primates might be more diverse than previously thought, with potential implications for ecological and evolutionary host-parasite associations, as well as epidemiological dynamics.

In the second study, I investigate whether strongyles found in Bornean primates are the nodule worm *Oesophagostomum* spp., and to what extent these parasites are shared among members of the community. To test this, I propose two hypotheses that use the parasite genetic structure to infer transmission processes within the community. In the first scenario, the absence of parasite genetic substructuring would reflect high levels of parasite transmission among primate hosts, as primates' home ranges overlap in the study area. In the second scenario, the presence of parasite substructuring would suggest cryptic diversity within the parasite genus and the existence of phylogenetic barriers to cross-species transmission. By using molecular markers, I identify strongyles infecting this primate community as *O. aculeatum*, the only species of nodule worm currently known to infect Asian nonhuman primates. Furthermore, the little to no genetic substructuring supports a scenario with no phylogenetic barriers to transmission, and where host movements across the landscape would enable gene flow between host populations. This work shows that the parasite's high adaptability could act as a buffer against local parasite extinctions. Surveys targeting human populations living in close proximity to nonhuman primates could help clarify whether this species of nodule worm presents the zoonotic potential found in the other two species infecting African nonhuman primates.

Finally, **chapter 6** focuses on the most abundant parasites in the community, STH, an ever-present and often neglected component of terrestrial host communities. A wide range of biotic and abiotic factors influence their distribution; their reproduction and dispersal depend largely on the probability of successful transmission to a host, while the survival and development of their infectious stages (eggs and larvae) are predominantly influenced by abiotic variables. Numerous studies have focused on the determinants of parasite infection in various taxa, but fewer studies have explored what influences the distribution of STH at a landscape level. Here, I examine the spatial distribution of three groups of STH infecting Bornean primates in an area that corresponds to one of the most primate-diverse regions in Borneo, with up to ten primate species living sympatrically. I conducted primate surveys along the river and collected fecal samples for morphological characterization of parasite stages shed in feces. Landscape attributes were extracted from open data sources and delimited to the study area. Using generalized linear mixed models, I provide evidence that low

primate diversity and disturbed areas are associated with higher STH abundance, indicating that diverse host communities can depress parasite populations, *i.e.* biodiversity dilutes infection risk. This study highlights the role of ecological and environmental factors shaping host-parasite associations, and offers a starting point to future investigations of spatial parasite ecology in natural systems.

Through a community-level approach, this thesis attempts to reduce the knowledge gap on what we currently know about primate parasitism in natural systems. In addition to cataloging the drivers of parasite diversity and distribution, understanding patterns of host specificity and generalism is critical to our ability to predict how anthropogenic change is impacting and will continue to impact host-parasite associations.